

---

# ECTOMYCORRHIZAE: CO-EVOLUTION, SIGNIFICANCE, AND BIOGEOGRAPHY<sup>1</sup>

---

Roy E. Halling<sup>2</sup>

## ABSTRACT

The fungus/plant root association known as a mycorrhizal symbiosis appears to have evolved in the Devonian. Of the two general morphological types of mycorrhizae among plant families, arbuscular mycorrhizae appear earlier in the fossil record and are more widespread than are ectomycorrhizae. The latter type of symbiosis most likely evolved with the vascular plant progenitors of modern Pinaceae in the Jurassic, but also developed with the ancestors of a dozen or so extant Angiosperm families. The significance of the ectomycorrhizal relationship is evident in that the symbionts profit by acquiring resources from their partners that would otherwise be unavailable. In natural environments where ectomycorrhizal communities exist, the symbiosis may be restricted or not depending on the particular plants and fungi involved. The presence of an obligate specificity of a particular fungus with a particular plant has a profound consequence on biogeographic distribution.

*Key words:* Australia, biogeography, Colombia, Costa Rica, disjunct distribution, fungi, montane tropics, mycorrhizae, symbiosis.

---

I address five general points regarding mycorrhizae below, with particular reference to the type known as ectomycorrhizae. These points are: (1) mycorrhizae, (2) the organisms involved, (3) co-evolution, (4) biological significance, and (5) biogeography. The discussion is not from the viewpoint of one who studies the mycorrhizal phenomenon, but rather as a mycotic systematist whose study organisms frequently form these mycorrhizal associations.

### (1) MYCORRHIZAE

Mycorrhiza refers to an association/symbiosis/mutualism between plants and fungi wherein fungi colonize the cortical tissue of feeder rootlets during periods of active rootlet growth. The movement of plant-produced carbon to the fungus and fungal-acquired nutrients to the plant generally characterizes the association. Equally important are the production of growth regulators by the fungi, the protection of rootlets from pathogen invasion or heavy metal uptake, and the provision of sporocarps as food for mycophagous animals. The term "mycorrhiza," comes from the Greek "mykes + rhiza," which means *fungus-root* and was first applied to fungus-tree asso-

ciations described in 1885 by A. B. Frank (1885). According to Trappe (1977a: 203), "About 95 percent of the world's present species of vascular plants belong to families that are characteristically mycorrhizal; mycorrhizae have evolved as the norm of terrestrial plant nutrition, not the exception." A clearinghouse for mycorrhiza information on the WWW can be found at: <http://mycorrhiza.ag.utk.edu>. Also, an updated text by Smith and Read (1997) provides an excellent overview of the subject.

Although mycorrhizae exhibit several different types of morphologies, I will address just one: the ectomycorrhiza. In terms of species numbers, the fungi predominately involved in the association are Homobasidiomycota (mushrooms, puffballs, and allies), although some Ascomycota are also important ectomycorrhiza-formers (including truffles and the pervasive *Cenococcum*). Among other features of the Homobasidiomycota, the spore-producing cell of these fungi, the non-septate basidium, is a hallmark of the group. The diagnostic feature of an ectomycorrhiza is the presence of hyphae between the root cortical cells producing a netlike structure called the Hartig net. By definition, ectomycorrhizae have a sheath, or mantle, of fungal tissue that

---

<sup>1</sup> Much of the work has been supported by the National Science Foundation (BSR 86-00424) and by the Office of Forestry, Environment and Natural Resources, Bureau of Science and Technology, of the U.S. Agency for International Development in NSF Grant No. DEB-9300798. The advice and aid of many interested parties in Latin America made much of the fieldwork possible. I am particularly grateful to Gregory Mueller, Field Museum of Natural History, for his continued collaboration over the past decade. Finally, I want to thank the director and staff of the Missouri Botanical Garden for providing the opportunity to present some of this material in oral form at their annual systematics symposium.

<sup>2</sup> Institute of Systematic Botany, The New York Botanical Garden, Bronx, New York 10458-5126, U.S.A.

may completely cover the absorbing root (typically the fine feeder roots). The mantle can vary widely in thickness, color, and texture depending on the particular plant-fungus combination. The mantle increases the surface area of absorbing roots and often affects fine-root morphology, resulting in bifurcate, pinnate to irregular, or coralloid branching. Sometimes hyphal strands extend into the soil from the mantle. Often hyphae aggregate to form rhizomorph-like strands that may be visible to the unaided eye. The internal portion of these strands can differentiate into tubelike structures specialized for long-distance transport of nutrients and water. A color atlas of specific ectomycorrhizal morphologies can be found in Agerer (1987–1999). In some associations, persistent intracellular penetration of the cortical cells occurs in which case the association is called an ectendomycorrhiza. One form of this type of mycorrhiza known as “arbutoid” occurs with some members of the Ericaceae and has characteristics of both ectomycorrhizae and endomycorrhizae. Intracellular penetration occurs in the root cortex, a mantle forms, and a Hartig net is present. These associations are found on *Arbutus* (e.g., Pacific madrone), *Arctostaphylos* (e.g., bearberry and manzanitas), and several species of the Pyrolaceae. In the monotropoid subtype, the fungi colonize achlorophyllous (lacking chlorophyll) plants in the Monotropaceae (e.g., Indian pipe and Snow plant), producing the Hartig net and mantle.

## (2) THE ORGANISMS INVOLVED

Ectomycorrhizae are found on certain woody plants. They are worldwide in distribution and are particularly adapted to habitats with marked seasonal changes, especially where periodic flushes of nutrients occur in the soil. One estimate (Molina et al., 1992) states that between 5000 and 6000 fungal species, belonging primarily to the Homobasidiomycota (at least 25 families according to Miller, 1982), and fewer to the Ascomycota ( $\pm 9$  families), are known to form ectomycorrhizae. Many of these fungi produce mushrooms, puffballs, truffles, and false truffles on the forest floor. Some fungi are restricted to a single plant species, like *Suillus grevillei* (Klotzsch) Singer on larch, *Truncocolumella citrina* Zeller on Douglas fir, or *Suillus spraguei* (Berk. & Curt.) Kuntze on eastern white pine. In contrast, others have a very broad host range, such as *Pisolithus tinctorius* (Pers.) Coker & Couch, which will form ectomycorrhiza with more than 40 tree species belonging to at least eight genera. We know that a single plant, or plant species, usually forms ectomycorrhizae simultaneously with many

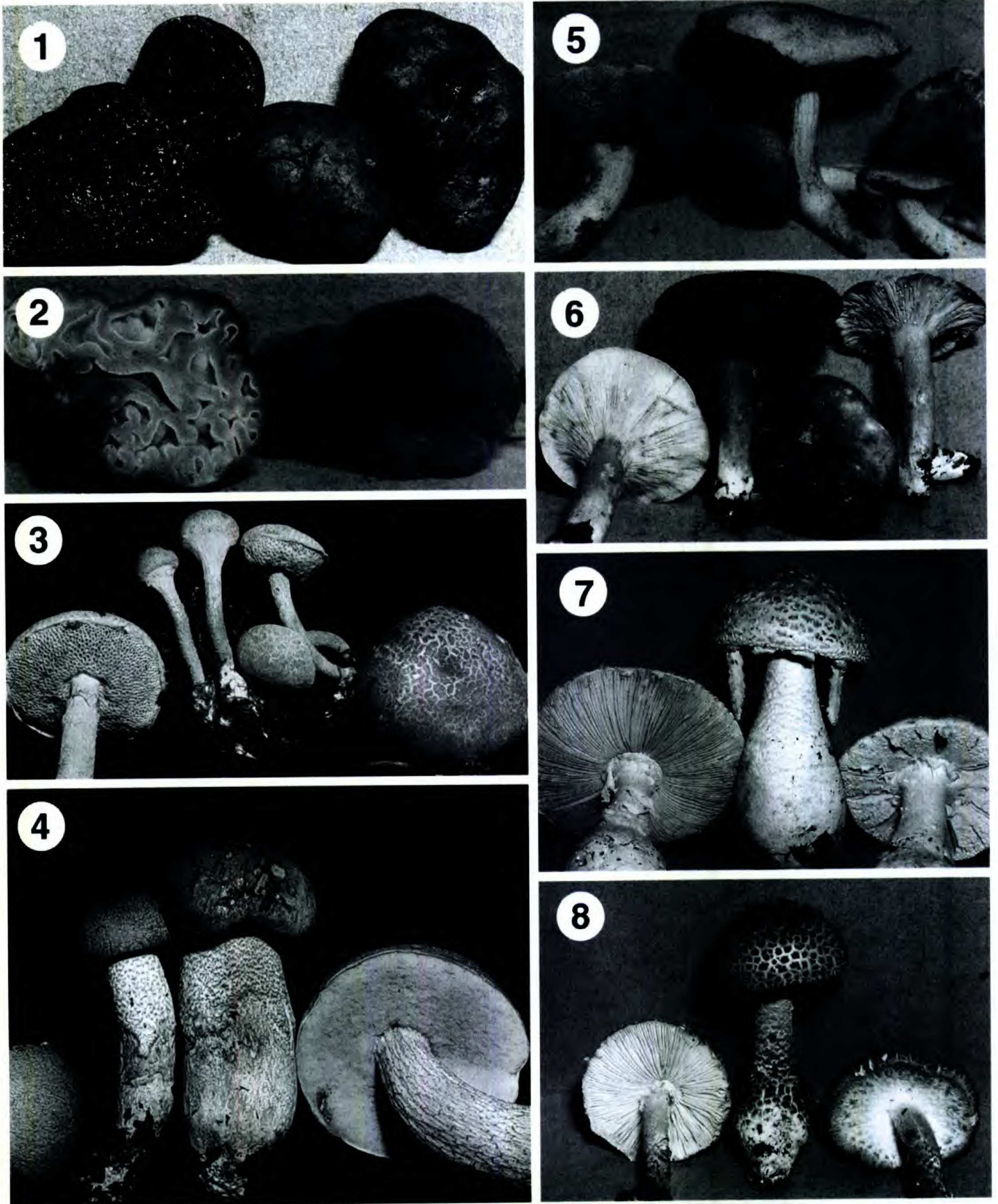
different fungi at the same time in the same place, and a succession of different fungi occurs over the lifetime of a plant. In the case of Douglas fir, an important timber resource in the western U.S.A., mycorrhizists at the U.S.D.A. Forestry Laboratory in Corvallis, Oregon (Molina et al., 1992) estimate that around 2500 fungi associate with that tree, some exclusively, some not.

Only about 3% of phanerogams form ectomycorrhizae (Meyer, 1973). While this number is relatively small in terms of overall numbers of vascular plants, the global importance is tremendous because of their disproportionate occupancy of the land surface and their economic value as timber sources. Most of the plants, such as members of the Pinaceae and Fagaceae, dominate forests outside of the tropics along with eucalypts and other Myrtaceae in temperate and tropical Australasia, and dipterocarps, which dominate forests of tropical Indo-malaya. Considerable recent work shows that many caesalpinoid legumes are ectomycorrhizal on nutrient-poor soils in the lowland tropics of Africa and South America and will form canopy-dominant stands (Alexander, 1989; T. Henckel, pers. comm.) in which they do not support nitrogen-fixing bacteria. Also, in the montane Neotropics, recent north temperate immigrants such as oak and alder occupy areas in which they are the dominate canopies (Kappelle, 1996). It is of interest to note that the ectomycorrhizal fungal genera associated with these trees are also of north temperate origin (see below).

## (3) CO-EVOLUTION

It has been postulated that fungi were critical in the transition of ancient plants from aquatic habitats to land by enhancing water and nutrient uptake as well as decomposition of substrates and development of soils in rather harsh landscapes (Malloch et al., 1980; Bougher & Tommerup, 1996). The earliest fossil mycorrhiza dates from  $\sim 410$  mya, suggesting that the mycorrhizal way of life was well established by the Devonian.

Trappe (1977b) and Trappe et al. (2000) postulated that the present disjunct distribution of truffle-like fungi in Europe and North America (Figs. 1, 2) that sporulate underground (and depend on animals for dispersal) is best explained by their widespread occurrence throughout Laurasia prior to the tectonic events that broke up the animals' overland migration routes some 50 mya. While it is commonly accepted that aboveground forms (mushroom-producing agarics) are ancestral to those that produce truffle-like sporocarps (e.g., Thiers, 1984; Bruns et al., 1989; Mueller & Pine, 1994), those



Figures 1–8. Habits of false-truffles and mushrooms. —1. *Alpova* sp. ( $\times 1$ ). —2. *Hydnotrya tulasnei* ( $\times 0.75$ ). —3. *Pulveroboletus ravenelii* ( $\times 1$ ). —4. *Tylopilus chromapes* ( $\times 0.5$ ). —5. *Tylopilus queenslandianus* ( $\times 0.75$ ). —6. *Lactarius costaricensis* ( $\times 0.75$ ). —7. *Amanita conara*, nom. prov. ( $\times 0.3$ ). —8. *Amanita costaricensis*, nom. prov. ( $\times 0.3$ ).

mushroom-forming fungi that form ectomycorrhizae would have had to originate at some point before the 50 myr mark. Based on molecular clock dating of nuclear small-subunit ribosomal DNA sequences, Berbee and Taylor (1993) suggested that divergence of the Homobasidiomycota occurred in the

Triassic,  $\sim 220$  mya  $\pm 50$  myrs. If the Pinaceae (95% of which form ectomycorrhizae fide Newman & Reddell, 1987) are assumed to be monophyletic and plesiomorphically ectomycorrhizal, then the existence of *Compsostrobus*, a late Triassic fossil that is thought to be an ovulate cone of Pinaceae

(Delevoryas & Hope, 1987), could possibly indicate that ectomycorrhizal Homobasidiomycota might have arisen by ~200 mya. The oldest fossils of ectomycorrhiza are 50-myr-old associates of *Pinus* roots from the Princeton chert of British Columbia (LePage et al., 1997; Hibbett et al., 1997a). The fungal component is morphologically similar to the extant truffle-like genus *Rhizopogon*, but the true identity remains unknown because of a lack of the diagnostic spore-producing stage. Ectomycorrhizal fungi probably concomitantly diversified in the Jurassic, when ectomycorrhizal Gymnosperms were globally establishing a presence (before the break-up of Pangaea). The subsequent diversification of Angiosperms probably catalyzed a boost in the diversity of ectomycorrhizal fungi soon after these plants appeared in the Cretaceous (146–65 mya) (Raven & Axelrod, 1974; Talent, 1984; Truswell et al., 1987).

The recent discovery and eventual description of *Archaeomarasmius*, a possible member of the Tricholomataceae fide Hibbett et al. (1997a) from mid-Cretaceous New Jersey amber, suggest, at the very least, that an extant mushroom morphology existed at a minimum of 90–94 mya. Taking that date and the probable date of another fossil agaric, *Coprinites* (15–30 mya), and dated attine ant fossils (15–30 mya) (both in Dominican amber) and mapping these on the attine/fungus molecular co-phylogeny produced by Chapela et al. (1994), Hibbett et al. (1997a) hypothesized minimum divergence dates for nodes of that phylogeny. They suggested that the primarily ectomycorrhizal families (basal to the rest of the phylogeny) Boletaceae and Russulaceae could date from at least the mid-Cretaceous (90 mya) when Angiosperms appeared. According to Hibbett and Thorn (2000), by mapping ectomycorrhizae as a feature on a molecular phylogeny of Homobasidiomycota (Hibbett et al., 1997b), it appears possible that the ability to form ectomycorrhizae could have arisen eight different times. However, they indicate that this inference is weak due to insufficient sampling of taxa.

*Suillus* s.l. and *Rhizopogon* are the two largest genera in the suilloid group of mushrooms and false-truffles (of the Boletaceae). According to Bruns et al. (pers. comm.), most larger clades and grades within these genera, and the radiation at large, are associated with subgroups of white pine or red pine, Douglas fir, or larch, but these specific associations are convergent. They estimate the timing of the suilloid radiation at 60 to 35 mya (Eocene), which is recent relative to the origin of genera in the Pinaceae (late Triassic). This timing difference and the convergence of host-pattern ar-

gues against co-cladogenesis. Nevertheless, host fidelity within the suilloids is high over evolutionary time scales, and host-switching events are rare and usually restricted to a suite of closely related plant genera. However, speciation of the fungi within a taxonomic suite of plant associates is common. In North America, there are  $\pm 10$  spp. of *Suillus* [e.g., *S. serotinus* (Frost) Kretzer & Bruns] associated only with *Larix*, for example. At the extreme, as I mentioned before, there are estimates that there may be over 2500 species of ectomycorrhizal fungi associated with Douglas fir (Molina et al., 1992). Some fungi will be found only with that tree (e.g., *Truncocolumella citrina*), while others can associate with members of other genera and families of plants.

The fungi of the Monotropaceae, a plant family consisting of achlorophyllous epiparasites, also form ectomycorrhizae with nearby coniferous trees and thereby form a link through which carbon and other nutrients can flow from the autotrophic host plant to the heterotrophic, epiparasitic plant. Using DNA fingerprinting techniques, Cullings et al. (1996) demonstrated in the monotropes that *Sarcodes sanguinea* Torr. (Snow plant) appeared to be a generalist in its fungal associations, while *Monotropa uniflora* L. (Indian pipe) from widely divergent habitats associated exclusively with members of the Russulaceae. *Monotropa hypopithys* L. was more specialized in associating with *Suillus* and/or *Rhizopogon*. *Pterospora andromeda* Nutt. from several geographic regions was at the extreme, forming mycorrhizae only with *Rhizopogon subcaerulescens* A. H. Smith, a false-truffle. The authors (Cullings et al., 1996: 64) "... argue that the specificity resulted from a one-sided selection on these parasitic plants to increase their fitness by optimizing carbon allocation, rather than from co-evolution in the sense of reciprocal selection." What are the benefits of such a specialization that outweighs the loss of opportunity provided by a generalist strategy? They hypothesize that the suilloid fungi, in specialization with Pinaceae, have become more efficient at obtaining carbon from their partners, and that the most widespread monotropes in those pine ecosystems have in turn specialized on the most efficient conduit of fixed carbon.

Largent et al. (1980a) showed that *Amanita gemmata* (Fr.) Gillet formed ectendomycorrhizae with manzanitas (*Arctostaphylos* spp.) and ectomycorrhizae with lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in two different populations. In another study, Largent et al. (1980b) demonstrated the variability of type of ectomycorrhizae formed by species of Ericales. Some of each mycorrhizal type:

ecto, arbutoid, or ericoid could be found on the same plant species, madrone (*Arbutus menziesii* Pursh.), for example.

#### (4) BIOLOGICAL SIGNIFICANCE

Pirozynski and Malloch (1975: 154) speculated that the appearance of plants on land could only have happened through the establishment of a mycorrhizal symbiosis; it had to be a new lifestyle, a way uniquely capable of conquering a hostile habitat, "... a biological innovation on a scale equal to or surpassing that responsible for the Cambrian 'explosion'." This association allowed for increased efficiency in nitrogen and phosphorus uptake and was necessary for the exploitation of new habitats and development of more complex tissue systems (Pirozynski & Malloch, 1975). According to Malloch et al. (1980, and references cited therein), it seems clear that ectomycorrhizae conferred a selective advantage on the plants, making it possible for them to occur in pure or nearly pure stands in marginal habitats (such as at high elevations or latitudes, very poor soils, and/or areas with dramatic seasonal climatic shifts). Clearly, ectomycorrhizal associates have selective value in extreme environments because of their direct role in breaking down leaf litter and a more specialized and controlled recycling of nutrients back to the plants (Malloch et al., 1980, and references cited therein).

By effectively colonizing a larger volume of soil than plant roots do alone, the benefits that plants accrue from mycorrhizal symbioses can be generally characterized by increased growth and yield and improved fitness. For example, it has been documented that mycorrhizae affect phosphorus nutrition in plants (Allen, 1991). The fungus benefits directly from a link to a proven carbon source (and becomes a carbon sink according to M. Allen, pers. comm.). In any case, the benefit to both associates arises primarily because mycorrhizal fungi critically link plant roots with the soil. The mycorrhizal hyphae in the soil: (1) take up mineral nutrients from the soil solution and transport those nutrients to the root; and (2) release nutrients from the litter/humus layers by the production of enzymes involved in mineralization of organic matter. In this regard, we are talking about the breakdown of cellulosic and complex lignosic compounds by the fungus to be utilized by other soil organisms or the plant. By the first mechanism, a mycorrhiza increases the effective absorptive surface area of the plant's feeder roots. In nutrient-poor or moisture-deficient soils, nutrients and water taken up by the soil hyphae can lead to improved plant growth and

subsequent reproduction. As a result, mycorrhizal plants compete and tolerate environmental stresses better than non-mycorrhizal plants. These physiological benefits have been well documented in many case studies over the past several decades (Smith & Read, 1997).

In much of the northern spotted owls' range, old growth conifer forests provide relatively high densities of their preferred prey, the northern flying squirrel and the red-backed vole. Ninety percent of these rodents' diet consists of ectomycorrhizal, underground, truffle-like fungi in these large, dense forests of the Pacific Northwest (Hayes et al., 1986; Maser et al., 1978, 1985). The occurrence and benefit of mycorrhizal fungi in this forest community has been well described (Molina et al., 1992). Thus, in this situation, we see a tight, four-part harmony in which a bird species preys on rodent species that eat truffle-like mycorrhizal fungi which, in turn, are responsible for maintaining the health of Douglas fir trees whose branches and trunks provide prime roosting and nesting sites for the bird. As is often the case, charismatic macrofauna, like the owl, become the icon for conservation of unique and pristine ecosystems, yet experimental evidence verifies that ectomycorrhizal fungi are the actual keystone organisms (Amaranthus et al., 1989; Lamont, 1992; Grove & LeTacon, 1993; Read, 1993). Since the squirrel can adapt to laboratory rations and the vole cannot because of dentition, squirrel mycophagy is likely adaptive whereas the vole appears to represent co-evolution (Trappe, pers. comm.).

The previous example is not an isolated incident; small animal mycophagy has been documented for more than 20 years (Trappe & Maser, 1977; Fogel & Trappe, 1978). Similarly, there is additional documentation of similar feeding habits in less mesic environments by at least two Australian marsupials (brush tail rat kangaroo and southern brown bandicoot), which consume truffle-like fungi that form ectomycorrhizae with *Eucalyptus* (Malaczjuk et al., 1987). A comprehensive review of Australian mammal mycophagy has been extensively documented by Claridge et al. (1996). According to Andrew Claridge (pers. comm.), the Australian sooty owl consumes the mycophagous bush rat, as a core component of its diet, as well as the long-nosed bandicoot, which is notorious for consuming ectomycorrhizal fungi. Here is an analogous predator/prey/plant/fungus relationship in the Southern Hemisphere.

#### (5) BIOGEOGRAPHY

While my co-workers and I have been documenting ectomycorrhizal associations and distri-

butions during the last two decades, we have noticed some distinctive patterns: (1) relictual disjunct distribution of (A) an individual species, (B) a species group, and (C) a genus; and (2) generic and specific distributions along a cline.

#### (1) RELICTUAL DISJUNCT DISTRIBUTIONS

(A) Based on its current distribution, *Pulveroboletus ravenelii* (Berk. & Curt.) Murrill (pers. obs.) (Fig. 3), with basidiomata of variable size, exhibits a relictual disjunct distribution. I would suggest that it most likely has an ancient genome with minor phenotypic change, and is a generalist in its mycorrhizal associations. It partners with Pinaceae and various dicot genera in eastern and western North America. In its southern distribution in the Americas, *P. ravenelii* associates solely with *Quercus*. It is also reported from Fagaceae forests in southeastern Asia, dipterocarps in Indo-Malaya (Corner, 1972), Myrtaceae and Casuarinaceae in Queensland, Australia (pers. obs.), but is notably absent in Europe (pers. obs.).

(B) *Tylopilus* subg. *Roseoscabra* presents a different scenario (the *T. chromapes* group fide Wolfe & Bougher, 1993). Eight species were added by those authors to the original *T. chromapes* (Frost) Smith & Thiers (Fig. 4), including one (*T. cartagoensis* Wolfe & Bougher) from a *Quercus* forest in Costa Rica and two [*T. queenslandianus* Wolfe & Bougher (Fig. 5) and *T. palumanus* Wolfe & Bougher] from Myrtaceae and Casuarinaceae forests in northeastern Australia among others from east Asia (Japan and China). Wolfe and Bougher (1993) speculated that there was a Laurasian origin of the ancient genotype and subsequent migration to and speciation in Australia during Pleistocene glaciations via land bridges. Today known associates of subgenus *Roseoscabra* are Pinaceae, Fagaceae, Betulaceae, Salicaceae, Myrtaceae, Mimosaceae, and Casuarinaceae (distributions in the eastern United States, Costa Rica, Japan, and China to northeastern Australia; the subgenus is absent in Europe). Again, I hypothesize that we are probably looking at an ancient genome, a generalist mycorrhizal proclivity, but with some phenotypic change or genetic drift/allopatric speciation.

(C) Bougher et al. (1994) indicated that the obligate ectomycorrhizal mushroom *Rozites* essentially has a Gondwanan distribution. The genus seems to have most likely co-evolved with a Cretaceous fagalean complex with more genetic diversity going south (18 species known today), where it co-evolved with *Nothofagus* (Australia, New Zealand, Chile, Argentina, New Caledonia, Papua New

Guinea) and/or with Myrtaceae (in Australia). Lesser diversity for *Rozites* evolved in the Northern Hemisphere (only 3 species) and occurred after the continental breakup. We know that *Nothofagus* was distributed across southern Australia when it rafted away from Antarctica, but gradually went extinct in part of its range with increasing aridity across the region known as the Nullarbor Plain. Fossils of *Nothofagus* on that continent and its existence in South America and elsewhere have been the subject of much biogeographical debate (see references cited in Bougher et al., 1994). When *Nothofagus* went extinct in southwestern Australia (known also for its enigmatic flora) in the Eocene/Pliocene, Bougher et al. (1994) speculated that the relictual *R. symeae* Bougher et al. apparently jumped ship (switched hosts) from *Nothofagus* to relictual species of *Eucalyptus*. Interestingly, and not coincidentally, there is another species, *R. fusipes* Horak & Taylor (apparently a sister taxon to *R. symeae* fide Bougher et al., 1994), associated with *Nothofagus* in New Zealand and with *Nothofagus* and *Eucalyptus* in Tasmania. In the laboratory, Bougher (1987) demonstrated pure culture synthesis of ectomycorrhizae with *Nothofagus* and *Eucalyptus* using isolates of *Descolea maculata* Bougher & Malajczuk from Western Australia eucalypt forests. In the New World, Halling (1989) and Mueller and Strack (1992) have documented similar host shifts of mushroom species from conifers in the United States to oaks in Colombia and Costa Rica.

#### (2) GENERIC AND SPECIFIC DISTRIBUTIONS ALONG A CLINE

In the New World montane tropics, especially Costa Rica and Colombia, Greg Mueller and I (and our collaborators) have been documenting the macrofungus diversity (e.g., Halling & Ovrebo, 1987; Halling, 1996; Halling & Mueller, 1999; Mueller, 1996; Mueller & Halling, 1995; <http://www.nybg.org/bsci/res/hall/costaric.html>). Although we are not the first to note affinities of montane Neotropical Agaricales with taxa in the North Temperate zone (see Moser & Horak, 1975), we do suggest co-migration of mycorrhizal communities; that is, obligate ectomycorrhizal fungal genera have migrated from the North Temperate zone with their associated phanerogams, specifically alder and oak, both of which had a North Temperate origin. Palynological studies by Hooghiemstra and Cleef (1995) around Bogotá, Colombia, suggest that oak communities have been in the northern Andes less than 350,000 years and alder less than 1 million years.

A general analysis of phenetic similarities in one family and three genera of ectomycorrhizal mushrooms showed greater (at higher taxonomic levels) or lesser (at lower taxonomic levels) affinities with North Temperate taxa of the Western Hemisphere (Mueller & Halling, 1995). These data indicate a definite north/south clinal distribution pattern in four different ways.

- North temperate to southern Colombia: *Cortinarius iodes* Berk. & Curt., *Lactarius indigo* (Schw.) Fr., *L. atroviridis* Peck, *Laccaria amethystina* Cooke, *Strobilomyces confusus* Singer. These species have the largest distribution range.
- North temperate, south to Costa Rica: *Asterophora parasitica* (Fr.) Singer, *Boletus frostii* Russell, *Lactarius psammicola* A. H. Smith, *Lactarius rimosellus* Peck, *Russula nigricans* (Bull.: Fr.) Fr., *Tylopilus eximius* (Peck) Singer. *Nota bene* (N.b.), *Asterophora* is an obligate parasite of the obligately ectomycorrhizal *Russula*.
- Neotropical oak endemics: *Amanita garabitoana*, nom. prov., *Laccaria gomezii* Mueller & Singer, *Lactarius costaricensis* Singer (Fig. 6), *Leccinum andinum* Halling, *Rozites colombiana* Halling & Ovrebo. N.b., these genera are widespread north temperate entities, but these particular species appear endemic to the montane Neotropics.
- Restricted endemics (currently): *Amanita conara*, nom. prov. (Fig. 7), *A. costaricensis*, nom. prov. (Fig. 8), *Boletus flavoniger* Halling et al., *Leccinum talamancae* Halling et al., *Tricholopium violaceum* Halling & Franco-M. N.b., the genera are widespread north temperate taxa, but these species seem restricted to only a few sites in the Cordillera Talamanca of Costa Rica.

#### SUMMARY

Mycorrhizal associations have been around for a long time, at least since life forms migrated to terrestrial habitats. As these new habitats or niches became available, fungal and plant partners, both symbionts together as a community, likely explored and exploited new niches for resources. Some host-specific fungi and plants have co-evolved in earnest and migrated together, to a greater or lesser extent, over the millennia depending on habitat availability and the existence of potential partners. This fungus-plant union that occupies most of the terrestrial part of our planet would appear responsible for the very appearance of the earth's natural landscape.

#### Literature Cited

- Agerer, R. (Editor). 1987–1999. Colour Atlas of Ectomycorrhizae: With Glossary. Einhorn Verlag, Schwäbisch-Gamünd. 2 vols. (loose-leaf).
- Alexander, I. J. 1989. Systematics and ecology of ectomycorrhizal legumes. *Advances in Legume Biology. Monogr. Syst. Bot. Missouri Bot. Gard.* 29: 607–624.
- Allen, M. F. 1991. *The Ecology of Mycorrhizae*. Cambridge Univ. Press, Cambridge.
- Amaranthus, M. P., J. M. Trappe & R. J. Molina. 1989. Long-term forest productivity and the living soil. Pp. 36–52 in D. A. Perry et al. (editors), *Maintaining the Long-term Productivity of Pacific Northwest Forest Ecosystems*. Timber Press, Portland.
- Berbee, M. L. & J. W. Taylor. 1993. Dating the evolutionary radiations of the true fungi. *Canad. J. Bot.* 71: 1114–1127.
- Bougher, N. L. 1987. *The Systematic Position and Ectomycorrhizal Status of the Fungal Genus Descolea*. Ph.D. Thesis, University of Western Australia, Perth.
- & I. C. Tommerup. 1996. Conservation significance of ectomycorrhizal fungi in Western Australia: Their co-evolution with indigenous vascular plants and mammals. Pp. 299–308 in S. D. Hopper et al. (editors), *Gondwanan Heritage: Past, Present and Future of the Western Australian Biota*. Surrey Beatty & Sons, Chipping Norton.
- , B. A. Fuhrer & E. Horak. 1994. Taxonomy and biogeography of Australian *Rozites* species mycorrhizal with *Nothofagus* and Myrtaceae. *Austral. Syst. Bot.* 7: 353–375.
- Bruns, T. D., R. Fogel, T. J. White & J. D. Palmer. 1989. Accelerated evolution of a false-truffle from a mushroom ancestor. *Nature* 339: 140–142.
- Chapela, I. H., S. A. Rehner, T. R. Schultz & U. G. Mueller. 1994. Evolutionary history of the symbiosis between fungus-growing ants and their fungi. *Science* 266: 1691–1694.
- Claridge, A. W., M. A. Castellano & J. M. Trappe. 1996. Fungi as a food resource for mammals in Australia. Pp. 239–267 in K. Mallett & C. Grgurinovic (editors), *Fungi of Australia, Vol. 1B. Australian Biological Resources Study*, CSIRO, Canberra.
- Corner, E. J. H. 1972. *Boletus* in Malaysia. Government Printing Office, Singapore.
- Cullings, K. W., T. M. Szaro & T. D. Bruns. 1996. Evolution of extreme specialization within a lineage of ectomycorrhizal epiparasites. *Nature* 379: 63–66.
- Delevoryas, T. & R. C. Hope. 1987. Further observations on the late Triassic conifers *Compsostrobus neotericus* and *Voltzia andrewsii*. *Rev. Palaeobot. Palynol.* 51: 59–64.
- Fogel, R. & J. M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. *Northw. Sci.* 52: 1–31.
- Frank, A. B. 1885. Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. *Ber. Deutsch. Bot. Ges.* 3: 128–145.
- Grove, T. S. & F. Le Tacon. 1993. Mycorrhiza in plantation forestry. Pp. 191–227 in I. C. Tommerup (editor), *Advances in Plant Pathology, Vol. 9. Mycorrhiza Synthesis*. Academic Press, London.
- Halling, R. E. 1989. A synopsis of Colombian boletes. *Mycotaxon* 34: 93–113.
- . 1996 (1997). Boletaceae (Agaricales): Latitudinal biodiversity and biological interactions in Costa

- Rica and Colombia. *Revista Biol. Trop.* 44: (supplement 4): 111–114.
- & G. M. Mueller. 1999. New boletes from Costa Rica. *Mycologia* 91: 893–899.
- & C. L. Ovrebo. 1987. A new species of *Rozites* from oak forests of Colombia with notes on biogeography. *Mycologia* 79: 674–678.
- Hayes, J. P., S. P. Cross & P. W. McIntire. 1986. Seasonal variability in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. *Northw. Sci.* 60: 250–257.
- Hibbett, D. S. & R. G. Thorn. 2000. Homobasidiomycetes. In: P. Lemke & D. J. McLaughlin (editors), *The Mycota, Vol. VII. Systematics and Evolution*. Springer-Verlag, New York (in press).
- , D. Grimaldi & M. J. Donoghue. 1997a. Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of Homobasidiomycetes. *Amer. J. Bot.* 84: 981–991.
- , E. M. Pine, E. Langer, G. Langer & M. J. Donoghue. 1997b. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. *Proc. Natl. Acad. Sci. U.S.A.* 94: 12002–12006.
- Hooghiemstra, H. & A. M. Cleef. 1995. Pleistocene climatic change and environmental and generic dynamics in the north Andean montane forest and páramo. Pp. 35–49 in S. Churchill, H. Balslev, E. Forero & J. Luteyn (editors), *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden Press, Bronx.
- Kappelle, M. 1996. *Los Bosques de Roble (Quercus) de la Cordillera de Talamanca, Costa Rica: Biodiversidad, Ecología, Conservación y Desarrollo*. Univ. Amsterdam & Instituto de Biodiversidad.
- Lamont, B. B. 1992. Functional interactions within plants—The contribution of keystone and other species to biological diversity. Pp. 95–127 in R. J. Hobbs (editor), *Mediterranean Ecosystems in Australia*. Surrey Beatty & Sons, Chipping Norton.
- Largent, D. L., N. Sugihara & A. Brinitzer. 1980a. *Amanita gemmata*, a non-host specific mycorrhizal fungus of *Arctostaphylos manzanita*. *Mycologia* 72: 435–439.
- , ——— & G. Wishner. 1980b. Occurrence of mycorrhizae on ericaceous and pyrolaceous plants in northern California. *Canad. J. Bot.* 58: 2274–2279.
- LePage, B. A., R. S. Currah, R. A. Stockey & G. W. Rothwell. 1997. Fossil ectomycorrhizae from the Middle Eocene. *Amer. J. Bot.* 84: 410–412.
- Malajczuk, N., J. M. Trappe & R. Molina. 1987. Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. *Austral. J. Ecol.* 12: 53–55.
- Malloch, D. W., K. A. Pirozynski & P. H. Raven. 1980. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review). *Proc. Natl. Acad. Sci. U.S.A.* 77: 2113–2118.
- Maser, C., J. M. Trappe & R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59: 799–809.
- Maser, Z., C. Maser & J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Canad. J. Zool.* 63: 1084–1088.
- Meyer, F. H. 1973. Distribution of ectomycorrhizae in native and man-made forests. Pp. 79–105 in G. C. Marks & T. T. Kozłowski (editors), *Ectomycorrhizae*. Academic Press, New York.
- Miller, O. K., Jr. 1982. Taxonomy of ecto- and ectendomycorrhizal fungi. Pp. 91–101 in N. C. Schenck (editor), *Methods and Principles of Mycorrhizal Research*. Amer. Phytopathol. Soc., St. Paul, Minnesota.
- Molina, R., H. Massicotés & J. M. Trappe. 1992. Specificity phenomena in mycorrhizal symbiosis: Community-ecological consequences and practical implications. Pp. 357–423 in M. F. Allen (editor), *Mycorrhizal Functioning*. Chapman & Hall, London.
- Moser, M. & E. Horak. 1975. *Cortinarius* Fries und nahe verwandte Gattungen in Südamerika. *Beih. Nova Hedwigia* 52: 1–628.
- Mueller, G. M. 1996 [1997]. Distribution and species composition of *Laccaria* (Agaricales) in tropical and subtropical America. *Revista Biol. Trop.* 44: (supplement 4): 131–135.
- & R. E. Halling. 1995. Evidence for high biodiversity of Agaricales (Fungi) in neotropical montane *Quercus* forests. Pp. 303–312 in S. Churchill, H. Balslev, E. Forero & J. Luteyn (editors), *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden Press, Bronx.
- & E. M. Pine. 1994. DNA data provide evidence on the evolutionary relationships between mushrooms and false truffles. *McIlvainea* 11(2): 61–74.
- & B. A. Strack. 1992. Evidence for a mycorrhizal host shift during migration of *Laccaria trichodermophora* and other agarics into Neotropical oak forests. *Mycotaxon* 45: 249–256.
- Newman, E. I. & P. Reddell. 1987. The distribution of mycorrhizas among families of vascular plants. *New Phytol.* 106: 745–751.
- Pirozynski, K. A. & D. W. Malloch. 1975. The origins of land plants: A matter of mycotrophism. *Biosystems* 6: 153–164.
- Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- Read, D. J. 1993. Mycorrhiza and plant communities. Pp. 1–31 in I. C. Tommerup (editor), *Advances in Plant Pathology—Mycorrhiza Synthesis*. Academic Press, London.
- Smith, S. E. & D. J. Read. 1997. *Mycorrhizal Symbiosis*, 2nd ed. Academic Press, San Diego.
- Talent, J. A. 1984. Australian biogeography past and present: Determinants and implications. Pp. 57–93 in J. J. Veevers (editor), *Phanerozoic Earth History of Australia*. Clarendon Press, Oxford.
- Thiers, H. D. 1984. The secotioid syndrome. *Mycologia* 76: 1–8.
- Trappe, J. M. 1977a. Selection of fungi for ectomycorrhizal inoculation in nurseries. *Annual Rev. Phytopathol.* 15: 203–222.
- . 1977b. Biogeography of hypogeous fungi: Trees, mammals, and continental drift. 2nd Int. Mycol. Cong. Abstr. P. 675.
- & C. Maser. 1977. Ectomycorrhizal fungi: Interactions of mushrooms and truffles with beasts and man. Pp. 165–179 in T. Walters (editor), *Mushrooms and Man, an Interdisciplinary Approach to Mycology*. USDA Forest Service, Oregon.
- , M. A. Castellano & A. W. Claridge. 2000. Continental Drift, Climate, Mycophagy, and the Biogeography of Hypogeous Fungi. *Proc. 5th Congrès Int. Sci. et Culture de la truffe, Aix-en-Provence* (in press).
- Truswell, E. M., A. P. J. Kershaw & I. R. Sluiter. 1987. The Australian-southeast Asian connection: Evidence



---

from the paleobotanical record. Pp. 32–49 in T. C. Whitmore (editor), *Biogeographical Evolution of the Malay Archipelago*. Oxford Univ. Press, Oxford.

Wolfe, C. B., Jr. & N. L. Bougher. 1993. Systematics,

mycogeography, and evolutionary history of *Tylopilus* subg. *Roseoscabra* in Australia elucidated by comparison with Asian and American species. *Austral. Syst. Bot.* 6: 187–213.